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Influences of dietary protein level, amino acid supplementation and environmental temperature on performance, body composition, organ weights and total heat production of growing pigs[1]

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ABSTRACT: The study was conducted to determine the effects of feeding a 16% CP diet, a 12% CP diet, or a 12% CP diet supplemented with crystalline Lys, Trp, and Thr (12% CP + AA diet) in a thermal-neutral (23°C) or heat-stressed (33°C) environment on various body and physiological measurements in growing pigs. Heat-stressed pigs were given a 15% lower daily feed allowance than thermal-neutral pigs to remove the confounding effect of feed intake caused by high temperature. No diet × temperature interaction was observed for any variables ($P \geq 0.09$) except for pig activity and pancreas weight. At 33°C, pig activity and pancreas weight did not differ among dietary treatments ($P > 0.05$). In contrast, at 23°C, pigs fed the 12% CP diet had greater activity than those fed the 16% CP diet or the 12% CP + AA diet ($P < 0.05$). Pancreas weight was greater for pigs fed the 12% CP + AA diet than those fed the 12% CP diet ($P < 0.05$) when maintained at 23°C. Compared with 23°C, the 33°C temperature decreased pig activity, heat production, daily gain, feed efficiency, and affected the concentration and accretion of empty body protein and ash, as well as weights of heart, pancreas, stomach, and large intestine ($P < 0.05$). Pigs fed the 12% CP + AA diet attained similar levels of performance and rates of empty body water, protein, lipid, and ash deposition as pigs fed the 16% CP diet ($P \geq 0.10$). Pigs fed the 12% CP + AA diet had lower serum urea plus ammonia nitrogen concentrations ($P < 0.01$) and total heat production ($P < 0.05$) compared with those fed the 16% CP diet or the 12% CP diet. These results confirm that, with crystalline AA supplementation, growing pigs fed a 12% CP diet will perform similar to pigs fed a 16% CP diet. The data further indicate that lowering dietary CP and supplementing crystalline AA will decrease total heat production in growing pigs whether they are housed in a thermal-neutral or heat-stressed environment.

Key Words: Amino Acids, Growth, Heat Production, Pigs, Temperature

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Introduction

The use of low-CP diets supplemented with crystalline AA can reduce feed costs and N excretion in swine production. The increased fatness in pigs fed low-CP, AA-supplemented diets (Kerr et al., 1995; Knowles et al., 1998) may be partially due to more dietary energy being available for body fat synthesis as a result of reduced energy expenditure for catabolizing excess dietary protein. Excessive intake of CP has been shown to increase energy expenditure due to increased N excretion (Buttery and Boorman, 1976; Noblet et al., 1987; Le Bellego et al., 2001), as well as impacting organ size (Chen et al., 1999) and consequently energy metabolism (Koong et al., 1985; Yen, 1997; Nyachoti et al., 2000). The reduced plasma urea N in pigs fed low-CP, AA-supplemented diets (Lopez et al., 1994; Kerr and Easter, 1995) is another indication of a reduced energy need for the deamination of excess AA.

To reduce total heat production **(HP),** heat-stressed pigs voluntarily decrease feed intake (Nienaber et al., 1987a; Quiniou et al., 2000; Le Bellego et al., 2002) to lower heat increment **(HI)** associated with feed consumption. It is theorized that, through dietary CP reduction and AA supplementation, lean growth efficiency in heat-stressed pigs may be partially improved by lowering energy expenditure to dispose excess AA.

[1]Mention of a trade name, proprietary product, or specific equipment does not constitute a guarantee or warranty by the USDA and does not imply approval to the exclusion of other products that may be suitable.

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Improved performance under conditions of heat stress from diets formulated to minimize AA excesses has been observed in pigs (Stahly et al., 1979; 1991). Nevertheless, measurements of total HP in those studies were not conducted until recently (Collin et al., 2001a,b; Le Bellego et al., 2002).

The objectives of the present studies were to determine the effects of dietary CP level and AA supplementation on various physiological (serum urea N, physical activity, and total HP) and body variables (pig performance, body composition, and organ weights) in pigs maintained under the condition of thermal neutrality or heat stress.

Experimental Procedures

Twenty-four crossbred (¼ Chester White, ¼ Landrace, ¼ Large White, and ¼ Yorkshire) barrows were used in a 2 × 3 factorial arrangement of treatments. The factorial treatments comprised two environmental temperatures (thermal neutrality, 23°C or heat stress, 33°C) and three diets (a 16% CP diet, a 12% CP diet, or a 12% CP diet supplemented with crystalline Lys, Trp, and Thr **(12% CP + AA diet).** Pigs were weaned at approximately 4 wk of age and fed a common diet until allotment to treatment. Assignment to treatment was done randomly from outcome groups based upon weight, ancestry, and age. There were four replications of each treatment, with each replicate containing one pig. On each of eight consecutive days, three barrows were allotted, on alternate days, to either the 23°C or 33°C environments, and then randomly allotted to diet within environment. This procedure resulted from the availability of only three indirect calorimeters and ensured that each pig could have equal adaptation periods to each temperature × diet combination prior to total HP measurements (d 21 and 35 from initial treatment allotment) and final body composition analysis. Average initial and final weights were 23.4 and 36.0 kg, respectively, over the 36-d trial. All animal procedures were reviewed and approved by the U.S. Meat Animal Research Center Animal Care and Use Committee.

Diets (Table 1) were formulated using analyzed CP values for the corn and dehulled soybean meal. Nitrogen analyses of ingredients and diets were done by the macro-Kjeldahl procedure (AOAC, 1980) and CP was calculated (N × 6.25). Amino acid addition to the low-CP diet was based on the expected AA levels in the corn and dehulled soybean meal calculated from tabular values of the AA to CP ratios (NRC, 1988) and the analyzed CP level of each ingredient. Lysine and Thr concentrations of the diets were determined using ion-exchange chromatography (Beckman 119 CL amino acid analyzer, Palo Alto, CA) following hydrolysis of the samples in 6*N* HCl for 22 h at 100°C under a N atmosphere. Tryptophan analysis was by ion-exchange chromatography following alkaline hydrolysis of the samples as described previously (Sato et al., 1984). Lysine, Trp, and Thr additions to the 12% CP diet were made to equal the total levels calculated to be present in the 16% CP diet. Methionine plus Cys levels were not maintained according to NRC (1998) guidelines, but were formulated similar to diets used previously (Kerr and Easter, 1995; Kerr et al., 1995).

Table 1. Composition of diets, as-fed basis

	Dietary treatments		
Ingredient, %	16% CP	12% CP + AA	12% CP
Corn	76.35	85.60	86.20
Dehulled soybean meal	21.08	11.10	11.10
Dicalcium phosphate	1.08	1.28	1.28
Ground limestone	0.94	0.87	0.87
Trace mineral salt[a]	0.35	0.35	0.35
Vitamin mix[b]	0.10	0.10	0.10
Tylosin[c]	0.10	0.10	0.10
L-Lysine·HCl	—	0.38	—
L-Tryptophan	—	0.06	—
L-Threonine	—	0.16	—
Chemical composition, %			
Crude protein			
Calculated	16.00	12.00	12.00
Analyzed	16.20	12.98	12.26
Lysine			
Calculated[d]	0.87	0.87	0.57
Analyzed	0.84	0.84	0.59
Tryptophan			
Calculated[d]	0.17	0.17	0.11
Analyzed	0.13	0.13	0.09
Threonine			
Calculated[d]	0.57	0.57	0.41
Analyzed	0.63	0.60	0.48
Methionine + Cysteine	0.57	0.46	0.46
Calcium	0.65	0.65	0.65
Phosphorus, total	0.55	0.55	0.55
ME, Mcal/kg	3.27	3.25	3.25

[a]Trace mineral mix provided per kilogram of diet: Se, 0.1 mg (Na_2SeO_3); I, 0.35 mg (CaI_2); Cu, 8 mg ($CuSO_4·5H_2O$); Mn, 20 mg (MnO); Fe, 90 mg ($FeSO_4·H_2O$); Zn, 100 mg (ZnO); NaCl, 2.87 g.
[b]Vitamin mix provided per kilogram of diet: vitamin A, 3,300 IU; vitamin D_3, 330 IU; vitamin E, 22 IU; menadione sodium bisulfate, 2.2 mg; riboflavin, 2.2 mg; d-calcium-pantothenate, 6.1 mg; niacin, 16.6 mg; choline chloride, 165.4 mg; vitamin B_{12}, 0.02 mg.
[c]Provided 11 mg of tylosin/kg of diet.
[d]Calculated values were based on analysis of ingredients for CP and AA:CP ratios for estimates of AA concentration. Crude protein analyses were 7.8% for corn and 47.8% for dehulled soybean meal.

Pigs were individually fed three times daily (0900, 1700, and 0100) to allow for optimal AA utilization (Cook et al., 1983; Batterham, 1984). To ensure that heat-stressed pigs would consume their feed allowance and thermoneutral pigs would have an adequate feed allowance, the daily feed allotment was based on live BW and environmental temperature, such that pigs in the 33°C environment were fed 3.2% of BW and pigs in the 23°C environment were fed 3.8% of BW. Feeding pigs at 3.8% of BW was selected based on past N balance and performance experiments, which suggest that pigs of similar BW will consume feed equivalent to approximately 5% of their BW. We then took 75% of this value to ensure that all feed would be consumed in the calorimeters. The 15% lower feed intake for the 33°C environment compared with the 23°C environment (3.2 vs.

3.8% of BW) was derived from the findings of Stahly et al. (1979) and our unpublished results (B. J. Kerr, personal communication). Pigs were weighed every third day, and the subsequent daily feed allotment was adjusted accordingly.

Each temperature-controlled environmental chamber was 4.9 × 5.2 × 2.6 m and was operated as described by Nienaber and Hahn (1983). The temperature sensor was located immediately above an empty pen with a calibrated hygrothermograph located adjacent to the sensor to monitor temperature and relative humidity settings. Temperatures were maintained at a constant level of either 23°C or 33°C, with dew points held at approximately 15°C. Within each environmental chamber, there were 12 1.2 × 0.6-m pens with 0.76-m-high solid sides and expanded metal floors located 0.9 m above the room floor. Plastic trays under each pen allowed constant urine collection and weekly removal of feces. Each pig had its own water supply. Lights in the environmental chambers remained on 24 h/d.

Measurement of total HP was obtained using indirect calorimeters as described in detail by Nienaber and Maddy (1985). Briefly, animals were placed in the calorimeters at 0800 and 1 h after moving animals to the calorimeters, when air measurements and animal activity were shown to be stabilized, measurements were begun. Oxygen consumption and CO_2 production were calculated every 10 min based on analyses of inlet air and exhaust air of the calorimeters. Additionally, two samples from each calorimeter were continuously collected in gasbags over the entire 22-h period. Analyses of the composite samples were completed at the end of the 22-h period after the analyzers were recalibrated. Overall system accuracies for O_2 and CO_2 measurements were within 2% variation as determined by combustion of alcohol in each calorimeter. Total HP of each pig was measured on d 21 and 35 from the initiation experimental treatments. Calorimeter temperature and relative humidity were maintained equal to that in the environmental chambers where pigs were housed for the entire experiment. Calorimeter temperature averaged 23°C (SD = 0.41) for pigs in the 23°C environment and 32.6°C (SD = 0.56) for pigs in the 33°C environment. Feed allocation while in the calorimeter was based on the pig weight taken immediately prior to placing the pig in the calorimeter.

Calorimeters were cleaned between each total HP measurement and verified for O_2 and CO_2 measurement accuracy using alcohol combustion prior to d 21 and 35 total HP measurements. Urine was collected from the calorimeter and analyzed for N to adjust total HP and respiratory quotient **(RQ)** values (Brody, 1945). Lights above the calorimeters remained on 24 h/d. Pig activity was videotaped for 22 h with cameras located outside of each calorimeter and a time-lapse video recording system with a sequential switcher to tape individual calorimeters at 40-s intervals. After calorimetry measurement was completed, the videotape was reviewed in its entirety, and activity was classified as lying, standing, or eating. Total time spent at each activity was then summed and divided by the total run time. The percentages of standing and eating activities were summed and considered to be active physical activity.

Prior to experimentation, four additional pigs with genetic backgrounds and initial BW similar to the 24 test pigs were slaughtered and analyzed for water, protein, lipid, and ash as described below. At the end of the second total HP measurement (9 h after the 0100 meal), pigs were anesthetized, bled, and killed so that organ and empty gastrointestinal tract weights could be obtained since changes in organ size can have profound implications on energy metabolism (Koong et al., 1985; Yen, 1997). After weighing, all body parts were placed into a plastic bag, frozen at –20°C, and then ground (model 1109, Weiler and Co., White Water, WI) three times successively through a die with 6-mm holes. Three subsamples, 200 g each, were obtained and frozen for further processing. From each frozen subsample, three 20-g slices were taken, placed in liquid N, and then pulverized in a stainless steel food processor. Analyses for protein (N × 6.25), water, total lipids, and ash were performed on a composite, pulverized sample for each pig (AOAC, 1980). A blood sample was taken at the time of slaughter for serum separation and analyzed for urea plus ammonia N **(SUN)** (kit No. 640, Sigma Diagnostics, St. Louis, MO). Empty body gain of water, protein, lipid, and ash were calculated based on initial body composition of the four pigs killed at the beginning of the experiment and final body composition of the pigs on test at the end of the experiment.

In situations where pigs did not consume all the feed offered in the calorimeter, calorimetry data for that period was treated as a missing variable. Analysis of variance for calorimetry data included period (d 21 and 35), replicate (three), and treatment (two temperatures × three diets) in the statistical model. All subsequent data were analyzed as a factorial arrangement of treatments in a randomized complete block design using the GLM procedure of SAS (SAS Inst., Inc., Cary, NC), with replicate and treatment included in the model. Means were separated by the least significant difference procedure.

Results

There was no interaction between environmental temperature and dietary treatment on pig performance, empty body composition, or empty body accretion rates ($P \geq 0.09$). By design, pigs housed in the 33°C environment consumed less ($P < 0.01$) feed than pigs housed in the 23°C environment (Table 2). The 33°C environment reduced ADG ($P < 0.01$) and gain:feed ratio ($P < 0.05$) of pigs. Despite differences in feed intake, SUN concentrations were not affected by environmental temperature ($P = 0.73$). Table 3 indicates that pigs housed in the 33°C environment had higher concentration of water ($P = 0.02$), but lower concentrations of protein ($P = 0.03$) and ash ($P < 0.01$) in their whole empty body than pigs

Table 2. Effect of temperature and diet on pig performance

Treatment[a]	Body weight, kg		Gain, g/d	Feed intake, g/d	Gain/feed, g/kg	SUN, mg/dL[c]
	Initial[b]	Final[b]				
23°C						
16%	22.6	38.9	451	1,076	420	17.6
12% + AA	22.1	36.8	407	1,032	393	15.0
12%	22.8	34.5	324	1,011	319	20.7
33°C						
16%	24.2	36.5	349	923	379	21.5
12% + AA	24.3	36.6	357	905	394	10.3
12%	24.4	32.8	234	849	275	23.7
Residual standard deviation	1.74	3.29	46.9	83.3	28.7	4.88
Main effects						
23°C	22.5	36.7	394	1,040	377	17.8
33°C	24.3	35.3	313	892	349	18.5
16%	23.4	37.6	400[d]	999	400[d]	19.6[d]
12% + AA	23.2	36.7	382[d]	968	394[d]	12.6[e]
12%	23.6	33.6	279[e]	930	297[e]	22.2[d]
Source of variation, *P*-value						
Temperature	0.02	0.33	0.01	0.01	0.04	0.73
Diet	0.89	0.08	0.01	0.31	0.01	0.01
Diet × temperature	0.93	0.81	0.55	0.91	0.25	0.20

[a]There were four observations per temperature × diet treatment except for pigs fed the 16% CP diet at 33°C where only three observations were obtained. AA = Lys, Trp, and Thr supplementation.
[b]Represents allotment BW and final BW obtained at the end of the second calorimeter period. Pigs were on test for 36 d.
[c]Serum urea plus ammonia nitrogen.
[d,e]Within a column, means without a common superscript differ ($P < 0.05$).

Table 3. Effect of temperature and diet on empty body composition and accretion rates

Treatment[a]	Empty BW, kg[b]	Final empty body composition, %				Empty body accretion, g/d[c]			
		Water	Protein	Lipid	Ash	Water	Protein	Lipid	Ash
23°C									
16%	35.9	60.31	16.55	19.18	3.35	238	71	96	14
12% + AA	33.9	59.46	16.54	19.29	3.48	202	64	99	14
12%	31.7	56.73	15.94	21.18	3.90	132	47	105	15
33°C									
16%	34.4	61.49	16.15	18.78	3.05	201	56	87	9
12% + AA	34.4	60.99	15.65	20.13	3.45	199	51	89	12
12%	30.7	58.48	14.50	22.60	3.44	105	23	81	8
Residual standard deviation	2.96	1.400	0.881	1.811	0.186	29.9	10.6	19.3	
Main effects									
23°C	33.9	58.83	16.34	20.52	3.58	191	61	100	14
33°C	33.2	60.32	15.43	19.88	3.31	169	43	85	10
16%	35.2[d]	60.90[d]	16.35[d]	18.98[d]	3.20[d]	220[d]	63[d]	91	11
12% + AA	34.2[d]	60.23[d]	16.10[d]	19.71[d]	3.47[e]	201[d]	59[d]	94	13
12%	31.2[e]	57.60[e]	15.22[e]	21.91[e]	3.67[e]	119[e]	35[e]	93	12
Source of variation, *P*-value									
Temperature	0.59	0.02	0.03	0.42	0.01	0.10	0.01	0.10	0.01
Diet	0.05	0.01	0.06	0.02	0.01	0.01	0.01	0.97	0.23
Diet × temperature	0.79	0.93	0.54	0.62	0.11	0.55	0.59	0.68	0.09

[a]There were four observations per temperature × diet treatment, except for pigs fed the 16% CP diet at 33°C, where only three observations were obtained. AA = Lys, Trp, and Thr supplementation.
[b]Represents the final empty BW obtained before processing.
[c]Calculated using the average composition of four pigs, 26.7 kg of live weight, and empty BW of 24.2 kg, with an analyzed empty body composition of 63.89% water, 16.40% protein, 16.32% lipid, and 3.42% ash applied to the initial weights represented in Table 2. Deposition rates represent the total 36-d period.
[d,e]Within a column, means without a common superscript differ ($P < 0.05$).

Table 4. Effect of temperature and diet on organ weights[a]

Treatment[a]	BLD, g/kg	HRT, g/kg	LVR, g/kg	KDY, g/kg	SPL, g/kg	PAN, g/kg	TMS, g/kg	ADR, mg/k	TRD, mg/kg	STO, g/kg	SMI, g/kg	LGI, g/kg	CAE, g/kg	MES, g/kg
23°C														
16%	45.26	3.84	20.27	3.76	1.56	1.79^{de}	3.28	67.29	87.92	8.10	24.43	17.10	1.81	7.77
12% + AA	45.22	4.08	19.75	3.28	1.40	1.88^{d}	3.71	61.96	99.66	7.42	25.02	17.21	1.90	7.20
12%	45.15	4.08	21.05	3.33	1.51	1.57^{ef}	2.96	65.52	81.75	8.29	26.73	18.34	1.69	7.88
33°C														
16%	46.01	3.64	18.76	3.51	1.42	1.42^{f}	2.77	57.65	73.29	6.10	22.66	14.90	1.32	5.45
12% + AA	40.81	3.77	19.85	2.93	1.38	1.53^{f}	3.77	58.85	90.12	6.49	22.91	16.65	1.66	6.64
12%	44.74	3.67	21.71	3.19	1.26	1.68^{def}	2.67	66.03	90.08	7.58	26.11	15.57	1.58	7.42
Residual standard deviation	5.187	0.324	1.614	0.382	0.173	0.168	0.454	6.769	13.894	0.731	3.074	1.884	0.355	1.629
Main effects														
23°C	45.21	4.00	20.36	3.46	1.49	1.75	3.32	64.92	89.78	7.94	25.39	17.75	1.80	7.62
33°C	43.86	3.70	20.11	3.21	1.35	1.54	3.07	60.84	84.50	6.72	23.89	15.70	1.52	6.50
16%	45.64	3.74	19.52	3.63^{g}	1.49	1.61	3.03^{b}	62.47	80.61	7.10^{e}	23.55	16.00	1.57	6.61
12% + AA	43.02	3.93	19.80	3.11^{h}	1.39	1.71	3.74^{c}	60.40	94.89	6.95^{e}	23.96	16.93	1.78	6.92
12%	44.95	3.87	21.38	3.26^{h}	1.38	1.63	2.81^{b}	65.77	85.91	7.94^{d}	26.42	16.95	1.63	7.65
Source of variation, *P*-value														
Temperature	0.55	0.04	0.72	0.14	0.08	0.01	0.22	0.18	0.38	0.01	0.27	0.04	0.08	0.13
Diet	0.61	0.56	0.09	0.05	0.48	0.49	0.01	0.31	0.17	0.04	0.18	0.57	0.52	0.47
Diet × temperature	0.61	0.83	0.45	0.85	0.43	0.02	0.48	0.38	0.27	0.24	0.88	0.50	0.60	0.50

[a]There were four observations per temperature × diet treatment, except for pigs fed the 16% CP diet at 33°C, where only three observations were obtained. Average initial weight, 23.4 kg; average final weight, 36.0 kg; pigs were on treatment for 36 d. AA = Lys, Trp, and Thr supplementation. BLD = blood; HTR = heart; LVR = liver; KDY = kidneys; SPL = spleen; PAN = pancreas; TMS = thymus; ADR = adrenals; TRD = thyroid; STO = stomach; SMI = small intestine; LGI = large intestine; CAE = caecum; MES = messentary. Weights expressed per kilogram of empty BW.

[b,c]Within a column, means without a common superscript differ ($P < 0.01$).

[d,e,f]Within a column, means without a common superscript differ ($P < 0.05$).

[g,h]Within a column, means without a common superscript differ ($P < 0.10$).

housed in the 23°C environment. Pigs maintained in the 33°C environment had lower accretion rates of water, lipid ($P < 0.10$), protein, and ash ($P < 0.01$).

As shown in Table 2, pigs fed the 12% CP diet grew more slowly and were less efficient ($P < 0.05$) than pigs fed the 16% CP diet or 12% CP + AA diet, whereas pigs fed the 12% CP + AA diet performed in a manner similar to pigs fed the 16% diet ($P > 0.05$). No differences in feed intake were noted due to dietary treatment ($P = 0.31$). Pigs fed the 12% CP + AA diet had lower SUN concentrations compared with pigs fed either the 16 or 12% CP diets ($P < 0.05$). Table 3 shows that pigs fed the 12% CP diet had smaller empty BW and lower concentrations of water and protein, but higher lipid concentration in empty body than those fed the 16% CP diet or 12% CP + AA diet ($P < 0.05$). The empty body ash concentration of pigs fed the 16% CP diet was lower than that of pigs fed the 12% CP + AA or the 12% CP diet ($P < 0.05$). The accretion rates of empty body water and protein were lower for pigs fed the 12% CP diet than for those fed the 16% CP diet or 12% CP + AA diet ($P < 0.05$). There were no dietary affects on accretion rates of empty body lipid and ash ($P \geq 0.23$). Empty body composition and accretion rates of water and protein, were similar ($P > 0.05$) between pigs fed the 16% CP diet or pigs fed the 12% CP + AA diet.

Organ weights of pigs are presented in Table 4. There were no temperature × diet interactions on organ weights ($P \geq 0.24$), except pancreas weight ($P = 0.02$). In the 23°C environment, pancreas weight was greater for pigs fed the 12% CP + AA diet than for pigs fed the 12% CP diet. But in the 33°C environment, dietary treatments had no effect on pancreas weight of pigs. There were main effects of environmental temperatures and dietary treatments on the weights of several organs. Compared with the 23°C temperature, pigs maintained at 33°C had reduced heart ($P = 0.04$), pancreas ($P = 0.01$), stomach ($P = 0.01$), and large intestine ($P = 0.04$) weights. The kidney weight of pigs fed the 16% CP diet was greater than that of pigs fed the 12% CP + AA or the 12% CP diet ($P < 0.10$). The thymus weight was greater for pigs fed the 12% CP + AA diet than for pigs fed the 16% CP or the 12% CP diet ($P < 0.01$). Pigs fed the 16% CP or 12% CP + AA diet had smaller stomach weights than pigs fed the 12% CP diet ($P < 0.05$).

As shown in Table 5, no temperature × diet interaction was detected in heat production and respiratory quotient ($P \geq 0.11$). Both temperature and diet affected the total HP of pigs. Heat production was lower in pigs housed in the 33°C environment compared with pigs maintained in the 23°C environment ($P < 0.01$). Pigs fed the 12% CP + AA diet had lower total HP compared with pigs fed either the 16 or 12% CP diet ($P < 0.05$). Diet also influenced the respiratory quotient of pigs. Pigs fed the 12% CP diet had a higher respiratory quotient than pigs fed either the 16 or 12% CP + AA diet ($P < 0.05$). Temperature interacted with diet on pig

Table 5. Effect of temperature and diet on animal calorimetry measurements[a]

Treatment	Heat production, kcal·d^{-1}·kg$^{-0.75}$	Respiratory quotient	Pig activity, min/d
23°C			
16%	164.5	1.18	247[cd]
12% + AA	160.0	1.16	293[c]
12%	167.1	1.19	380[b]
33°C			
16%	147.1	1.13	240[cd]
12% + AA	135.9	1.17	191[d]
12%	141.2	1.20	202[d]
Residual standard deviation	7.45	0.041	61.5
Main effects			
23°C	163.9	1.18	307
33°C	141.4	1.17	211
16%	155.8[e]	1.16[e]	244
12% + AA	148.0[f]	1.17[e]	242
12%	154.1[e]	1.20[f]	291
Source of variation, *P*-value			
Temperature	0.01	0.27	0.01
Diet	0.04	0.03	0.07
Diet × temperature	0.33	0.11	0.01

[a]There were eight observations per temperature × diet treatment combination, except for pigs maintained in the 33°C environment and fed the 16% CP and the 12% CP + AA diets, where only five observations were obtained. Average initial weight = 23.4 kg; average final weight = 36.0 kg; pigs were on treatment for 36 d. Calorimetry data consisted of two observations per pig on d 21 and 35 after initiation of experimental treatments with pigs averaging 29.1 and 35.6 kg, respectively, for each calorimeter period. AA = Lys, Trp, and Thr supplementation.

[b,c,d]Within a column, means without a common superscript differ ($P < 0.01$).

[e,f]Within a column, means without a common superscript differ ($P < 0.05$).

activity ($P < 0.01$). Compared with pigs receiving the 16% CP or 12% CP + AA diet, pigs fed the 12% CP diet exhibited an elevated level of activity in the 23°C environment, but a similar activity level in the 33°C environment.

Discussion

There were minor discrepancies between calculated and analyzed concentrations of Lys, Trp, and Thr in the diets of the present study. Although exact reasons are unknown, AA analysis is inherently variable (Fontaine and Eudaimon, 2000), especially for Trp (Sato et al., 1984). Both calculated Lys levels and the total sulfur AA **(TSAA):**Lys ratio of 0.53 of the present study were similar to previously conducted experiments (Kerr and Easter, 1995; Kerr et al., 1995) and met NRC (1988) recommendations for 15- to 35-kg pigs when the studies were conducted. It should be noted that those Lys levels and the TSAA:Lys ratio were slightly below the current NRC (1998) recommendations, which may have affected some of the growth performance results of the present study.

Daily feed allowance in the present study was reduced by 15% for pigs housed in the 33°C environment compared with pigs housed in the 23°C environment. This approach was chosen to ensure that heat-stressed pigs would completely consume their feed allowance and that thermoneutral pigs would receive adequate feed allowance. By doing so, the effect of voluntary feed intake and associated HI on total HP of heat-stressed pigs can be removed. Therefore, the impact of CP reduction and AA supplementation on factors other than feed intake can be demonstrated. The 15% difference in feed intake was based on the information reported by Stahly et al. (1979) and our unpublished data (B. J. Kerr, personal communication). In 24- to 59-kg growing pigs, Stahly et al. (1979) observed a 12 to 19% reduction in feed consumption in animals housed in the 35°C environment compared with the 22.5°C environment. In our unpublished study with 240 group-housed growing pigs, the ADFI during the 29- to 48-kg of BW period was reduced by 16% (1,677 vs. 1,997 g/d) in pigs housed in the 33°C environment vs. pigs housed in the 23°C environment. Recently, Le Bellego et al. (2002) also reported a 15% reduction in daily feed intake for pigs housed in a 29°C vs. a 22°C environment, whereas Collin et al. (2001a) reported a 30% reduction in voluntary feed intake when temperatures were increased from 23°C to 33°C. It should be kept in mind, however, that reductions in feed intakes are not linear and are dependent on BW, with high temperatures having a more negative effect in heavier pigs (Quiniou et al., 2000). In our experiment, pigs were weighed every third day and subsequent daily feed allotment was adjusted accordingly. Consequently, feed intake relative to BW in this experiment was 3.5 and 3.0% for pigs kept in the 23°C and 33°C environments, respectively (Table 2),

which was slightly below initial targets of 3.8 and 3.2%, respectively.

No dietary treatment × environment temperature interaction was detected for daily gain, feed efficiency (gain:feed), and serum urea N in the present study. Lopez et al. (1994) also reported no interaction between environmental temperature (thremoneutral vs. hot diurnal) and dietary treatment (intact CP vs. AA-fortified) on daily gain, feed intake, or plasma urea N in finishing pigs.

Housing pigs in the 33°C environment had reduced ADG and feed efficiency compared with housing pigs in the 23°C environment in the present study. These results are in agreement with Nienaber et al. (1987a) and Collin et al. (2001b), who noted a reduced feed efficiency when pigs were housed in the heat-stressed vs. thermoneutral environment. In contrast, Le Bellego et al. (2002) reported no change in feed efficiency in pigs maintained in a 29°C vs. a 22°C environment, and Nienaber et al. (1987a) observed a decreased daily gain with no difference in feed efficiency in pigs housed in a 25°C vs. 20°C environment. These discrepancies in feed efficiency response to elevated environmental temperature could be related to the levels of feed intake reduction. In the study of Le Bellego et al. (2002), the similar feed efficiency between heat-stressed and thermoneutral pigs was associated with a 15% feed intake reduction. In the study of Nienaber et al. (1987a) a 15% feed intake reduction was also associated with a similar feed efficiency between the 25°C and the 20°C environments. In contrast, feed intake was reduced by 30% in the study by Nienaber et al. (1987a) using a 30°C environment vs. a 20°C environment, and by 25% in the study by Collin et al. (2001b) using a 33°C environment vs. a 23°C environment. The greater reduction of feed intake reported by Nienaber et al. (1987a) and Collin et al. (2001b) and the low feed intake in this experiment relative to BW may have precipitated some deficiencies in energy and other essential nutrients and thus may have lowered feed efficiency in pigs fed at the high environmental temperature. In contrast, however, Collin et al. (2001b) reported that a 25% reduction in feed intake in pigs maintained at 23°C does not necessarily alter feed efficiency.

In the present study, heat-stressed pigs had a SUN concentration similar to thermoneutral pigs when measurements were taken after the 35-d test. In agreement with our results, Lopez et al. (1994) also observed no changes in plasma urea N concentrations for finishing pigs housed in a hot diurnal environment (27.7 to 35°C) compared with the thermoneutral environment (20°C) when measurement was conducted on d 28 of the test.

Using similar reductions in dietary CP, (Kerr et al., 1995; Knowles et al., 1998; Smith et al., 1999), dietary treatment typically has little impact on feed intake. In addition, Le Bellego et al. (2002) noted no difference in daily feed intake due to CP level in pigs kept in a 29°C environment. In the current experiments, pigs fed the 12% CP diet grew at a slow rate, whereas pigs fed the 12% CP + AA diet grew at a rate comparable with pigs fed the 16% CP diet. Similar growth rates between pigs fed a high-CP diet and a reduced CP + AA diet have been shown previously (Kerr et al., 1995; Tuitoek et al., 1997b; Knowles et al., 1998).

The lower SUN concentration in pigs fed the 12% CP + AA diet in the current study indicates a reduction in deamination from excessive, unused AA compared with the 16% CP or 12% diet. Similar decreases in blood urea N concentrations in pigs fed reduced CP + AA diets have been reported previously (Lopez et al., 1994; Kerr and Easter, 1995; Knowles et al., 1998).

No interactions between environmental temperature and dietary treatment were noted on empty whole body composition or empty body accretion of water, protein, lipid, or ash in the present study. This complements the performance data and is supported by Lopez et al. (1994), who reported no interaction between environmental temperature and dietary treatment on tissue accretion rates in finishing gilts.

In the present study, pigs in the 33°C environment had a greater concentration of water, but lesser concentrations of protein and ash in the empty body compared with pigs in the 23°C environment. These different chemical compositions between the heat-stressed and thermoneutral pigs do not agree with previous observations. Stahly et al. (1979) noted similar concentrations of water, protein, lipid, and ash in the carcasses for pigs in the 35°C and 22.5°C temperatures, whereas Nienaber et al. (1987b) reported that pigs in the 30°C temperature had greater concentrations of water, protein, and ash than pigs in the 20 and 25°C temperatures.

There is no ready explanation to reconcile these discrepancies in chemical composition among the various studies. The lesser accretion rates of empty body water, protein, lipid, and ash observed in the present study for pigs in the 33°C environment compared with those in the 23°C environment were the consequence of decreased daily gain resulting from reduced feed intake.

Dietary treatment of the present study caused dramatic alterations in whole empty body composition and accretion rates. The whole empty body of pigs fed the 12% CP diet contained less water and protein, but more lipid and ash compared with that of pigs fed the 16% CP diet or the 12% CP + AA diet. A reduction in protein content and an increase in lipid content have been reported by others (Noblet et al., 1987; Kerr et al., 1995). Corresponding to their lowered rate of growth and alterations in body composition, pigs fed the 12% CP diet exhibited lower rates of body water and protein accretion compared with pigs fed the 16% CP diet or the 12% CP + AA diet. Pigs fed the 12% CP + AA diet had body compositions similar to pigs fed the 16% CP diet, which is in agreement with previous studies (Lopez et al., 1994; Kerr et al., 1995; Knowles et al., 1998). The lack of differences in empty whole body accretions of water, protein, lipid, and ash between pigs fed the 16% CP diet and pigs fed the 12% CP + AA diet confirms the

similarities noted among growth rates and is supported by others (Lopez et al., 1994; Tuitoek et al., 1997a).

The decreased weights of stomach and large intestine in the heat-stressed pigs of the present study apparently are related to the 15% reduction of daily feed intake. In agreement with previous studies (Nienaber et al., 1987b; Lopez et al., 1994), the heart weight of heat-stressed pigs in the current study was also reduced. Unlike results from studies by Nienaber et al. (1987b) and Lopez et al. (1994), heat stress in the present study did not reduce the weights of pig's liver and kidneys. A lack of heat stress effects on weights of the liver and kidneys in pigs had also been reported by Stahly et al. (1979).

The reduction in kidney weight due to feeding lower protein diets in the present study was expected (Lopez et al., 1994; Kerr et al., 1995; Chen et al., 1999), indicating a lower workload on kidneys in terms of excreting nitrogenous wastes. In contrast to previous studies (Lopez et al., 1994; Kerr et al., 1995; Chen et al., 1999), feeding lower protein diets in the current study did not reduce liver weight in pigs. The absence of effects from feeding low-protein diet on liver weight in pigs has also been shown by Knowles et al. (1998). It is unclear why no consistent response in liver weight to feeding low protein diet exists among different studies. Neither is it well understood why supplementing AA to the low-protein diet in the present study resulted in increased thymus weight, as well as increased pancreas weight in heat-stressed pigs, but not in thermoneutral pigs. The general decrease in pancreas weight in pigs fed reduced CP, AA-supplemented diets compared with pigs fed the higher CP control diets (Ward and Southern, 1995) was not evident in our trial.

Total heat production includes the HP associated with feed consumption, maintenance, thermal regulation, and physical activity (NRC, 1981; 1998). Fuller and Boyne (1972), Verstegen et al. (1973), and Holmes (1974) reported that the level of feed intake could have a large impact on total HP in pigs. Therefore, one may argue that the lower total HP by pigs in the 33°C vs. 23°C environment in the present study was confounded by the 15% difference in feed intake between the two environmental temperatures. However, an additional effect of heat stress beyond feed intake reduction on total HP in pigs has been demonstrated recently (Brown-Brandl et al., 2000). In that study, the total HP of finishing pigs with a 13% feed intake reduction induced by heat stress was lower than that of pigs with the same reduction in feed intake (13%) housed in a thermoneutral environment. The 14% reduction in total HP associated with the higher environmental temperature observed in the present study was slightly less than the 22% noted by Collin et al. (2001a). Further research by this group (Collin et al., 2001b) demonstrated that the reduction in total HP at high environmental temperatures is not only caused by the reduction in feed intake, but also by differences in energy efficiency through a reduction in fasting heat production. This information indicates that the decreased total HP in heat-stressed pigs was mediated by mechanisms in addition to feed intake reduction, and that the treatment effects on total HP of pigs observed in the present study was unlikely confounded by the 15% difference in feed intake between the two environmental temperatures. The lower total HP of pigs fed the 12% CP + AA diet vs. pigs fed the 16% CP diet in the current study is similar to previous reports on total HP response to AA-supplemented, low-protein diets (Noblet et al., 1987; Le Bellego et al., 2001). With each gram decrease of dietary protein intake, a reduction in total HP by 1.8 or 1.7 kcal in growing pigs was observed by Noblet et al. (1987) and Le Bellego et al. (2001), respectively. This reduction in total HP can be attributed to a decrease in HI associated with the synthesis and excretion of urea from excess AA. This contention is supported by the lower SUN concentration and lower kidney weight observed in the present study in pigs fed the 12% CP + AA diet vs. those fed the 16% CP diet. However, Fuller et al. (1987) showed no difference in total HP between pigs fed a 15 or 30% CP diet. It is well recognized that a higher RQ may be related to a greater rate of fat deposition (Brody, 1945; Noblet et al., 1999). In the present study, pigs fed the 12% CP diet had both higher RQ and greater empty body lipid concentration compared with those fed the 16% CP diet or the 12% CP + AA diet. These results are consistent with the observation of increased fatness in pigs fed low-protein diets without AA supplementation (Noblet et al., 1987; Kerr et al., 1995).

In our previous study (Brown-Brandl et al., 2000), active physical activity (standing and eating) of pigs was decreased in heat-stressed vs. thermoneutral environments. Decreased physical activity is one of the mechanisms that pigs use to reduce thermogenesis in order to cope with elevated environmental temperature. Physical activity can represent up to 10% of the total HP in fasting growing pigs (van Milgen et al., 1998). A decline in physical activity in heat-stressed pigs fed the 12% CP + AA diet or the 12% CP diet was observed in the present study and can be explained as a response of pigs to elevated environmental temperature. Yet, it is difficult to interpret why no difference in physical activity was detected between heat-stressed and thermo-neutral pigs fed the 16% CP diet in the current study. In the thermoneutral environment, pigs fed the 12% CP + AA diet had lower physical activity and total HP than pigs fed the 12% CP diet, suggesting the lower physical activity could be a contributing factor for the observed lower total HP. This explanation, however, does not apply to pigs housed in the heat-stressed environment because no dietary effect on physical activity was detected, even though feeding 12% CP + AA diet resulted in a lower total HP. Apparently, factors other than physical activity were responsible for the lower total HP in heat-stressed pigs fed the 12% CP + AA diet. One possible factor could be decreased HP relating to catabolism and excretion of excessive, unused AA.

Serum urea nitrogen concentration is a variable for measuring the degree of excess AA catabolism. Feeding the 12% CP + AA diet to heat-stressed pigs produced lower serum urea nitrogen, as well as reduced total HP compared with 12 and 16% CP diets. Both lower serum urea nitrogen and reduced total HP were also found in thermoneutral pigs fed the 12% CP + AA diet. Furthermore, an indicator of the excretory function of kidneys is their weight. The weight of kidneys in pigs fed the 12% CP + AA diet was statistically less than that found in pigs fed the 16% CP diet and numerically less than that found in pigs fed the 12% CP diet in both heat-stressed and thermoneutral environments. These results provide unequivocal evidence for suggesting that the decreased total HP in pigs fed the 12% CP + AA diet was a consequence of reduced catabolism and excretion of excessive, unused AA. By lowering daily feed allowance by 15% for heat-stressed pigs to remove the confounding feed intake effect on total HP, the present study further demonstrates that the HP associated with catabolism and excretion of excess AA in pigs is an important factor contributing to the reduction in total HP at high ambient temperatures.

In conclusion, the present study confirms that, with supplementation of crystalline Lys, Trp, and Thr, growing pigs fed a 12% CP diet will have growth performance and lean tissue gain similar to those fed a 16% CP diet. The current study further demonstrates that, compared with those fed the low- or high-protein diet, growing pigs fed the low-protein diet supplemented with AA will have reduced SUN concentration, kidney weight, and total HP regardless of whether they are housed in a thermoneutral or heat-stressed environment. Apparently the reduced total HP and its energetic benefit from feeding an AA-supplemented, low-protein diet in the present study was insufficient to impact the metabolism of lean and fat tissues in growing pigs. This contention is based on the lack of differences in accretion rates of empty body protein and lipid between pigs fed the 16% CP diet and those fed the 12% CP + AA diet in the current study.

Implications

Lowering the dietary crude protein level and supplementing with certain crystalline amino acids is an approach to decrease nitrogen excretion in pigs, provided that growth performance and lean tissue gain are similar. As demonstrated in the present study, feeding diets with reduced protein and supplemental amino acids would also decrease total heat production by growing pigs maintained in thermoneutral or heat-stressed environments, and decrease nitrogen excretion, as reflected by lower kidney weights and serum urea plus ammonia nitrogen concentrations. The resulting energetic benefit, as noted in this short-term study, however, was insufficient to affect lean and fat tissue metabolism accretion rates in growing pigs.

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